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Do Naked Goby (Gobiosoma bosci) Larvae Exhibit Periodic Vertical Movements in Order to Facilitate Upriver Migration in the Hudson River Estuary?

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HONORS THESIS

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Abstract

Estuaries provide high quality nursery habitat for larval fishes due to high productivity, predator protection, and warm temperatures. Previous studies suggest that larval naked gobies (*Gobiosoma bosci*) are capable of upriver migration and estuarine retention despite net seaward flow. *Gobiosoma bosci* larvae were collected at a fixed site in the Hudson River estuary in late July of 1998 from 4 discrete depths to provide a time-series of depth-stratified abundance during both a spring and a neap tide. Larvae were concentrated at depth, indicating that depth preference behavior is present and will likely contribute to up-river transport. Harmonic regression analysis revealed that larvae are most abundant in samples at night due to periodic diel vertical migrations in which they move deeper than the sampled region during daytime. Dependent upon hydrography of this site, diel vertical movements may also contribute to up-river transport. Larval depth distribution was not homogenized by spring tide mixing. Large larvae were generally found deeper and moved over a greater vertical range than small larvae. A separate component of the sampling design involved collection of individuals from the length of the river over a series of several weeks. We are using growth rates established from otolith analysis to determine along-river movement rates of larval cohorts in order to allow determination whether the behaviors characterized in this experiment actually facilitate up-river movement.

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Introduction

Many fish species on the East Coast of North America use estuaries as nursery habitat during their early development. Relative to open coastal or pelagic habitats, estuaries provide greater predator protection (few large predators, lower encounter rate due to murkiness, more structured habitat in which to hide), high productivity, and warmer temperatures (Miller, Crowder et al. 1985). Whether larvae migrate into estuaries for growth (temperature, food) or survival (reduced predation pressure) advantages depends on species, but in most species it is probably advantageous in both respects.

To prevent being washed out of the estuary, larvae must engage in behaviors that facilitate retention or upriver migration (Boehlert and Mundy 1988). The costs of upriver migration include the need to osmoregulate over a wide salinity range and metabolic cost associated with swimming against the prevailing seaward flow The persistence of upriver migration indicates that the associated growth and/or survival benefits must outweigh the costs. By quantifying behaviors that affect distribution, it is possible to clarify when and where larvae are most vulnerable. The purpose of this study was to determine behaviors that are likely to facilitate upriver transport of naked goby (*Gobiosoma bosci*) larvae in the Hudson River estuary.

A variety of behaviors and physiological adaptations, depending on species and habitat, have evolved to reduce the costs of migration. Osmotic tolerance sufficient to adjust

to changing salinity over the course of migration is critical. Estuarine-resident species are particularly well suited in this regard because they are euryhaline organisms. Estuarine flow is characterized by salinity gradients that vary dramatically with tide, and estuarine-resident species have adapted strategies to use tidal flow to their benefit (Dovel 1971). If a species is already adapted to cope with a wide salinity range such as that associated with tidal mixing, there should not be much stress induced by the decrease in salinity as larvae would experience as they migrate upriver. In addition to physiological adaptations, individuals may also engage in behaviors that decrease the cost of migration. Two such behaviors are depth preference and periodic vertical movements.

Larvae can move upriver by spending more time in deeper waters due to a preference for depth or salinity (Boehlert and Mundy 1988; Hill 1991). The surface water layer is characterized by net seaward flow. Below this is a boundary layer of null longitudinal velocity in which average direction of flow is neither seaward nor landward. Still further down is the landward layer. A larva that remained only in the surface layer would be carried out to sea at approximately the rate of water flow minus any active swimming in the opposite direction. If it was able to remain at the null longitudinal boundary layer, a larva would essentially maintain longitudinal position. If estuarine retention or upriver transport is to be achieved through depth preference alone, the deep landward water layer is the best depth for a larva to spend most of its time. This behavioral mechanisms allows larvae to be carried upriver with far less energetic output than directed swimming.

Periodic vertical movements of larvae are also believed to facilitate upriver transport. There are two major cyclical periods of movement that are especially effective: diel and

tidal. Diel cycles in vertical movement occur when larvae have different daytime and nighttime depth preferences, possibly due to light requirements for feeding, predator avoidance, or demersal schooling behavior. Tidally induced cycles of vertical movement occur when larval abundance and depth distribution varies with tide. Tidal mixing affects prey distribution, and therefore possibly also affects the density of their larval predators. For example, distribution of herring larvae have been shown to be very closely correlated to distribution of microzooplankton (Fortier and Leggett 1983).

The larvae discussed in this thesis were spawned in early summer. During their larval stage, they will experience more hours of light than dark in a 24 hour period. Periodic diel migration would favor upriver transport if larvae remained deep during the long daytime period and moved upwards only for the shorter period of darkness. By spending most of their time in the deep landward water mass, larvae behaving in this manner will experience net upriver transport.

Selective tidal stream transport (STST) occurs when larvae move up toward the surface when a flood tide is moving water upriver (McCleave and Kleckner 1982). When the tide begins to ebb and pull the wedge of saltier water back out to sea, the larvae sink below the tidally-affected wedge. Then they wait at depth until the next flood tide occurs, at which time they rise to the surface again. By engaging in this cycle of utilizing flood and ebb tides, larvae may move upriver in a ratchet-like manner.

Because the speed and efficiency of upriver transport by each of these mechanisms is dependent upon interacting factors of complex flow, the determination of which strategy contributes most to upriver movement in a particular species and system is difficult to assess

without detailed data on time- and location-specific flow structure. A logical approach, as taken in this experiment, is to first determine patterns of depth distribution and from these patterns, determine which of the above mechanisms is likely to affect along-river transport. Follow-up studies can be refined to clarify flow and movement patterns on an appropriate scale.

In order to determine which mechanisms contribute to upriver transport of *G. bosci* in the Hudson River estuary, a number of statistical models to characterize behaviors of an abundant larval fish species were used. In order to understand the causes and ultimate effects of behaviors in which this species engages, it is necessary to know some details of its life history. The naked goby (*Gobiosoma bosci*) is an estuarine-dependent fish that has been found at salinities ranging from freshwater to 45 psu. Although it is a euryhaline organism, 96.7% of individuals in a survey of the Mississippi River were found between salinities of 1.28 and 13.86 psu (Rounsefell 1964). Reproducing adults require oyster reef habitat to spawn. The eggs are attached to the inside of hinged oyster shells and guarded by males (Wang and Kernehan 1979). Spawning occurs from May to September in the Middle Atlantic Bight. The eggs hatch into 2 - 3 mm larvae after a 5-day incubation period. Larvae remain planktonic from the time of hatching until they reach 12 – 15 mm and settle to a benthic habitat (Shenker, Hepner et al. 1983). The early life history of *G. bosci* is believed to be similar to that of many other estuarine-dependent or estuarine-facultative species. Recently hatched larvae move upriver after hatching and return downriver after spending time in the protected estuarine nursery habitat (Able and Fahay 1998).

The first evidence that larvae of naked gobies are transported upriver was based on an observation that small larvae in the York River were found unexpectedly far upriver from *G. bosci* spawning grounds (Massmann, Norcross et al. 1963). A pattern of upriver migration of *G. bosci* larvae has been demonstrated in the Patuxent River based on an upriver increase in larval length over eight weeks (Shenker, Hepner et al. 1983). In this study, larvae were shown to move upriver at a rate of approximately 1 km/day. Although selective tidal stream transport was proposed as the mechanism, it has not been experimentally tested. Although Shenker's experimental design did not allow for a determination of the mechanisms responsible for longitudinal movement, he suggested that larvae migrate upriver by selectively utilizing tides. The work conducted here was designed to determine whether *G. bosci* larvae of the Hudson River estuary engage in behaviors that might facilitate such movement by characterizing vertical movements and/or depth preference of larvae at a fixed site on a fine temporal scale. If a consistent pattern of vertical movement is demonstrated, it is possible to predict how this behavior is likely to interact with physical flow parameters and contribute to upriver transport. Otolith analysis allows aging of larvae and determination of how the median position of a cohort changes in along-river position over time.

Materials and Methods

Sample collection

In order to provide a fine temporal scale of sampling, *G. bosci* analyzed in this study were collected at a single site on the lower Hudson River (**Fig. 1**). The Hudson River runs through eastern New York state and flows into the Atlantic Ocean in Manhattan. Two

cruises were conducted such that one coincided with spring tide and one with neap tide. The cruises were separated by 2.5 days. Cruise 1 (abbreviated C1) was conducted during a spring tide for approximately 3 days, and was followed by cruise 2 (C2) for approximately 3.5 days during a neap tide (**Table 1**). All gobies that were analyzed for migratory mechanisms in this study were collected at river site 3 (henceforth RS3). Other sites in this area were used to sample bay anchovy, but will not be discussed herein. This site was in the shipping channel 55 km from the mouth of the river (latitude: 41.164^{o} N, longitude: 73.911^{o} W) where the average maximum depth is 14 m. This is an oligohaline and highly productive area of the river where high larval abundance was expected. Four depths (2, 4, 6, and 8 m) were sampled with a Tucker trawl (1 m^2 opening, 333 μm mesh) for approximately 3 minutes every 2 hours (**Fig**. **2**). Rate of flow was measured during each tow, allowing calculation of total volume sampled in order to determine larval densities. A CTD was deployed during each ichthyoplankton tow to record temperature, conductivity, and depth. The Tucker trawl also had a device on the release mechanism that recorded these parameters. Data collected by the release mechanism device was used for data analysis purposes in the second cruise after we determined from anomalous data that the CTD failed during the second cruise. The trawl was slowly pulled up to the surface to sample successively shallower depths after sampling at 8 m. Upon retrieval of the trawl, samples were immediately sieved and preserved in separate jars with 70% ethanol. The ethanol was changed once within the first 48 hours to protect sample quality.

Species identification

Two species of gobies are commonly found in the Hudson River: seaboard goby *(Gobiosoma ginsburgi*) and naked goby (*Gobiosoma bosci*)(Lippson and Moran 1974). The larvae are quite similar morphologically. *G. bosci* is distinguished by the presence of a vertical post-anal melanophore (Able and Fahay 1998). Ichthyoplankton samples collected during the cruises were first sorted and separated into vials by species. All *G. bosci* larvae within a sample were counted and examined under a dissecting microscope and classified as pre-flexion or post-flexion according to whether their notochord had undergone flexion. The larvae found in each sample were counted and transferred to a 2-dram vial.

Size class abundance and length calculations

Up to 50 individual larvae were selected randomly from each sample and measured. Selection of individuals was done by shaking the vials of larvae and removing larvae randomly with forceps until 50 were obtained. Standard length measurements were obtained with Optimas image analysis software and a digital camera connected to a dissecting microscope, allowing accurate measurement of small and/or bent larvae (**Fig. 3**).

At each depth, frequency of size class (in 1 mm classes) in the measured sub sample was multiplied by concentration in each sample to provide an estimate of abundance-by-size. This allowed comparison of relative abundance of 11 size classes (2 – 12 mm standard length). Lengths were logarithmically transformed to reduce heterogeneity of variance. Principal components analysis was done to determine whether there was significant between-sample variability in larval size. Our sampling covered a very short time frame, so in order to determine long-term trends in abundance of the species, we include data on *G. bosci* larvae and juveniles during yearly surveys by Northeast Utilities

(Associates 2000). Annual abundance of larval Gobiidae and juvenile *G. bosci* collected during utilities sampling were plotted to demonstrate how abundance of this species has varied in the Hudson River estuary in the past.

Test for depth preference

The depth distribution of larvae was characterized by estimating the mean abundance of larval size class at each sampled depth. Separate estimates were developed for spring (cruise 1) and neap (cruise 2) tide periods, and for different size classes of larvae.

Analysis of temporally variable distributions

To determine whether larvae were distributed differently at different times of day, as predicted by STST, three tidal periods known to be strong contributors to the complex flow structure of the Hudson River estuary were tested using harmonic regression. Tidal components tested included: M4 (6.2 hour period), M2 (12.4 hour period), and K1 (23.9 hour period). The diel (day/night) cycle has a period of 24 hours, which is very close to that of the K1 tide. The short duration of our cruises did not allow us to distinguish between K1 and diel signals. Seasonal effects were also included in the model to account for longer-term (i.e. >1 d) temporal trends; they were tested as a first-order (day, in seconds) and second-order (day^2) effects. Day was determined as difference from the mean time of each cruise (where mean time was the midway point in cruise duration), and was squared before calculating the second-order seasonal effect (day^2) to avoid colinearity between these variables.

Tidal components were entered into the model as $A * \cos(\omega t + \phi)$ where A is amplitude of periodic variability, ω is angular frequency of variability, and ϕ is phase shift

of variability relative to reference time, t_0. This formula was linearized so that regression analysis could be applied. Therefore, each tidal component was entered into the regression model with two components based on the overall linearized formula:

$$\cos(\alpha + \beta) = \cos(\alpha) * \cos(\beta) - \sin(\alpha) * \sin(\beta) \quad (1)$$

This formula provided two components of each tide to be tested for significant predictive power, and these correspond to the x and z components of the tidal predictors presented in ANOVA and regression statistic figures.

Harmonic regression was employed to test for periodic temporal variability on two components of larval distribution: larval abundance and larval depth distribution. Periodic variability in larval abundance could be the result of several processes, including, but not limited to, vertical migration. Vertical migration would affect abundance if there are at times an abundance of larvae in unsampled portions of the water column (i.e. close to the bottom, where the Tucker trawl was not operated), which migrate into sampled portions of the water column at other times. A further test of this possibility was conducted by performing harmonic regression on the temporal variability in depth distribution of larvae. The summary variable for depth distribution is the depth center of abundance, (abbreviated Zcm):

$$Zcm = \Sigma prtot / stot*mndepth \quad (2)$$

Where "stot" is sum of larvae per square meter of surface, "prtot" is proportion of stot taken at each mean depth, and "mndepth" is the depth at which the sample was taken. Separate harmonic regression analyses were conducted on each cruise/size class.

Growth analysis

In order to estimate growth rates based on larval length (to be used in later analysis of along-river transport patterns), age information was collected from individuals along the length of the estuary by counting daily growth increments on otoliths. Ichthyoplankton samples from along the length of the Hudson River were collected by Northeast Utilities (NU) in 1998 and 1999. Samples were chosen for otolith analysis based on river position, date, and preservation method. Samples from two dates each year (7/14 and 7/28 in 1998; 7/12-7/13 and 7/26 – 7/28 in 1999) were analyzed, based on when *G. bosci* was most abundant. Unfortunately, many of the samples had been preserved in formalin rather than ethanol when they were collected by NU and therefore could not be used for otolith analysis.

From samples collected during times when *G. bosci* larvae were most abundant, up to 20 specimens were selected for otolith analysis. In order to collect growth information from as wide a size/age range of larvae as possible, individuals within a sample were divided into four size classes and 5 individuals were selected from each size class sub sample for otolith extraction. Sagittal otoliths were extracted with insect dissecting pins under a dissecting microscope. Both sagittal otoliths from each individual were placed in a droplet of immersion oil on a slide and allowed to clear for at least 1 week before increments were counted. (This waiting period allowed the otoliths to absorb oil and therefore make the increments more distinguishable). In some cases, only one otolith could be extracted from an individual. Otoliths were examined under a 40x oil immersion lens (**Fig. 4**). Increment counts were taken twice independently on each otolith to ensure between-count precision. If both sagittal otoliths from an individual were extracted, the count was taken from the one

that was visually determined to be more readable. Sub daily increments were present on some otoliths, but they could usually be distinguished from daily increments by adjustment of the focus. Counts were taken from the primordium to the edge, along the longest axis of growth.

Daily growth increments obtained from otolith counts were regressed against individual length. An analysis of covariance (ANCOVA) was done to determine predictors of variability in growth rate. Based on significant predictors revealed by the ANCOVA, a regression was done to determine how much variability in growth rate (slope) can be explained by the significant predictors.

Results

Abundance of *G. bosci* larvae

The majority of samples collected from all depths during both cruises had zero gobies (**Fig. 5**). Larvae were more abundant in deeper sampled depths (**Fig. 6**). Larval density was calculated as mean logarithmic abundance of *G. bosci* larvae (number of individuals / volume of water sampled). The mean log density of larvae during cruise 1 was 0.90 log larvae/m^3 (N = 218 samples). Log density during cruise 2 was 0.69 log larvae/m^3 **(**N = 232 samples). These densities include samples containing zero *G. bosci* larvae. No *G. bosci* eggs were found in any sample.

Size structure

The mean length of young-of-year individuals over both cruises was 5.69; median length was 5.50 mm (**Fig. 7**). The smallest larva was 2.42 mm and the largest was 11.94

mm. All larvae collected during this sampling effort lacked the pigmentation normally developed after settling.

Principal components analysis revealed samples vary meaningfully in size structure by both depth and cruise. Ontogenetic change in behavior may be the underlying reason for variation in size structure between samples. To test this hypothesis, larvae were pooled into 2 sizes: small (less than 5 mm) and large (greater than or equal to 5 mm) for harmonic regression analysis.

Predictors of abundance

Table 2 shows which predictor variables had a significant effect on larval abundance. In cruise 1, depth and the M2 tide were significant predictors. In cruise 2, depth, time of day (dayt2), K1 tide, and M2 tide were significant predictors.

Depth distribution of larvae by size and cruise

Larvae were most abundant in deep water. Both large and small larvae collected at neap tide larvae occurred in highest abundance at 8 m. Large and small larvae during spring tide (C1) were most abundant at 6 m. The large larvae in both cruises were present at higher abundance at all depths (except 2 m, where there were few *G. bosci* larvae) than small larvae.

Temporal variability in larval abundance

Table 3 shows the results of ANOVAs (analysis of variation) that provides significant predictors (p-value <= 0.05) of temporal variability in larval abundance in our samples. There were no significant predictors for abundance of large spring tide larvae. Abundance of small spring tide larvae was weakly correlated with the M2 (12.4 hour period)

tide (R-square = 0.23). During neap tide, both small (R-square = 0.39) and large larvae (R-square = 0.48) were correlated to the K1 tide (23.9 hour period). Larval abundance of small and large larvae during neap tide was highest at midnight and lowest at noon (**Fig. 8**).

Temporal variability in depth center of distribution

An ANOVA for depth center of distribution indicated significant predictors for each cruise and size class (**Table 4**). The K1 tide was a significant predictor of depth center of distribution for large spring tide larvae (R-square = 0.58), small neap tide larvae (R-square = 0.33), and large neap tide larvae (R-square = 0.70). There was no significant variability in depth center of distribution of spring tide small larvae. The pattern of temporal variability in depth center of distribution was similar for the large spring and both classes of neap tide larvae: mean depth of larvae in a sample was shallowest at midnight and deepest at noon (**Fig. 9**). Small neap larvae were slightly shallower than large neap tide larvae at night, but large neap larvae were noticeably deeper at noon.

Increment count - length regression

The results of an ANCOVA to determine whether there is variance between slopes within a river run (2-week sampling period)/year grouping are shown in **Table 5**. River run 17 in 1998 had significant between-sample variance in slopes. Count-length regression revealed no significant difference in slope between years (**Table 6**). In 1998, there was more variability in size at age as well as more difference between increment counts of smaller individuals (**Fig. 10**). July 14 larvae were unusually small in 1999 compared to larvae of the same age in 1998 (**Fig**. **11**).

Discussion

These data suggest that larvae displayed two behaviors that could promote upriver migration: preference for depth and diel vertical migration. As shown in **Fig. 6**, *G. bosci* larvae clearly exhibited a depth preference during both spring and neap tide. This depth preference was particularly strong in large larvae, suggesting that this behavior develops as larvae become more capable of modifying their position. Depth preference behavior is likely an adaptive strategy for larger larvae to be more strongly associated with the benthic substrate that will settle onto as juveniles.

Temporal variability in larval abundance

The regression of variability in larval abundance revealed that there was significant temporal periodicity in the number of larvae caught in our samples during both tides. This suggested that, in addition to depth preference, periodic vertical movements might also be exhibited by larval *G. bosci*. During spring tide, there was no variability in abundance of small larvae and a weak 12.4 hour periodicity in abundance of large larvae was observed. During neap tide, both small and large larvae were most abundant in samples collected at midnight and least abundant in noon samples. Large neap tide larvae were more abundant at night than small neap tide larvae, but both had a similar minimum abundance at noon. The observed temporal variability in larval abundance suggests that many larvae beneath the deepest sampled region (8 m) during daytime. Because the mean maximum depth of the sampling site was 14 m, larvae moved into the 6 remaining meters that were unsampled.

Temporal variability in depth center of distribution

One of the questions of interest is why larval abundance varied with time. The strong depth preference of larvae observed here, combined with temporal variability in sample larval abundance, suggests that many larvae at RS3 were missed by our sampling because they were deeper than 8 m. Alternatively, larvae could have moved laterally to the eastern or western shoals of the river during the day, or they could have evaded the trawl better at day because there was higher light intensity.

In order to test our hypothesis that larvae moved beneath the sampled region during the day and back into it at night, a mean depth center of distribution was calculated for each sample and harmonically regressed these observed values against a model based on significant predictors. The results of this regression confirmed our hypothesis. Large spring tide larvae and both size classes of neap tide larvae exhibited deepest depth center of distribution at noon and shallowest at midnight. Many of the observed mean depth center of distribution values during neap tide were 8 m, indicating that larvae strongly preferred deep water and were therefore likely to be found even deeper than we sampled.

During neap tide, small larvae were generally found slightly shallower than large larvae at midnight, but large larvae were much deeper than small larvae at noon. This explains why the R-square for temporal variability in abundance of large neap larvae was greater than that of small neap larvae. It appears that large neap larvae move over a wider vertical range between day and night, so they are more likely than small neap larvae to move out of the sampling region and therefore vary more in abundance.

Adaptive significance of depth preference

Even when larvae were at their shallowest depth center of distribution, they were not near the surface. The shallowest larvae during neap tide at midnight were below 3.5 m. Large larvae clearly had a stronger depth preference than small larvae. It has been suggested that *G. bosci* larvae less than 8 mm SL may shoal demersally, but these individuals have low feeding rates (based on gut content analysis) and therefore their fate and behavior are perplexing (Breitburg 1991). Demersal shoaling behavior was observed in larvae as small as 6 mm both in the field and lab (personal observation as cited in Breitburg, 1991). In light of our discovery that *G. bosci* larvae move vertically, it is likely that these larvae do not remain at the bottom and starve. Rather, they probably remain at depth for most of the day to be transported upriver and then move shallower at night to feed.

G. bosci larvae probably do not shoal demersally for the immediate purpose of upriver transport. This species becomes completely benthic upon settlement, so adoption of demersal shoaling behavior of larvae may indicate an ontogenetic shift towards assumption of the benthic lifestyle. All demersal larvae observed on an oyster reef in the Chesapeake Bay were found within 0.5 m of the substrate or other physical structure (Breitburg 1989). In that study, larvae found near the oyster reef usually did not have food in their guts, indicating that demersal behavior is not an adaptation for feeding. All of the larvae that Breitburg collected from just above the oyster bar were collected at midday. About half had food in the reargue, but only one had food in the foregut. She suggested that feeding may have occurred nocturnally/crepuscularly on the reef or prior to movement to the reef. Our findings favor the second hypothesis because it explains that larvae move out of the landward deep water at night in order to feed. Other studies demonstrate age-related changes

in larval behavior. Rainbow smelt (*Osmerus mordax*) were shown to engage in species-specific use of the vertical water column (Laprise and Dodson, 1989). This difference in vertical distribution was correlated to a difference in longitudinal distribution.

Importance of transport mechanisms in *G. bosci*

Tidal transport (either selective or due to depth preference) is critical to the retention of larvae in estuaries. Larval fishes lack sufficient body mass to store large amounts of energy necessary for sustained directed swimming. Even if they did have the ability to migrate solely through their own active horizontal swimming, they would increase their risk of predation due to fatigue. Miller (Miller, Crowder et al. 1985) calculated the ability of immature spot (*Leiostomus xanthurus*) and croaker (*Micropogonias undulatus*) larvae to swim the course of their documented migration, 100 km in 50 days while growing from 2 mm to 15 mm. He suggested that it would be very unlikely for larvae to migrate this far without assistance from tidal currents, even if they exhibited ideal streamlining, lack of predation, and feeding efficiency. This calculation indicates that larvae must utilize an external force to move upriver after hatching.

Preference for deep water will almost definitely lead to upriver transport, but the contribution of diel vertical movements at this site are less clear. Without additional information on near-bottom flow in the Hudson River, it is difficult to determine whether the diel vertical movements that we observed at RS3 will contribute significantly to upriver transport. Under proper conditions, diel vertical movement of larvae will result in upriver transport because the diel cycle interacts with the principal solar semi-diurnal tidal constituent (S2) (Hill 1991). However, this model assumes that the difference between the

amplitudes of mid-water and near-bottom currents is greater than the difference between the amplitudes of mid-water and surface current. Because we do not have flow data from the bottom of the channel, we cannot confirm that those conditions were met at RS3.

Differences in hydrographical parameters of an estuary may influence the behavioral mechanisms that larvae employ to facilitate upriver transport. Such parameters are variable between estuaries and within an estuary over time. Most previous work on *G. bosci* is based on samples collected from the Chesapeake Bay and its tributaries (Shenker, Hepner et al. 1983),(Breitburg 1991). Unlike the Hudson River, the Chesapeake Bay region is subject to frequent episodes of anoxia at depth, due to combined effects of anthropogenic eutrophication and physical flow structure. Differences in dissolved oxygen (DO) levels between the Chesapeake Bay and the Hudson River may mean that *G. bosci* larvae in these systems are constrained by different mean dissolved oxygen levels and must adjust their transport-inducing behaviors accordingly. Newly hatched *G. bosci* have a TL_{50} oxygen concentration of 1.30 mg/l (Saksena and Joseph 1972). He found that half of larvae exposed to this DO level for 24 hours died. It is unlikely that the dissolved oxygen level would be this high in the Chesapeake for 24 hours because oxygenated water would flush the habitat on the incoming tide. However, there is a critical oxygen concentration of 0.50 mg/l, which could kill larvae before than the habitat could be re-oxygenated by tidal flow.

Anoxic and hypoxic conditions are generally most severe near the bottom of the water column. Even when dissolved oxygen is not lethally low, larvae may avoid such areas. When bottom-layer DO in the Patuxent River was <= 2 mg/l, larval *G. bosci* density was less than one-third of density when DO was above 2 mg/l (Keister, 2000). This three-

fold difference in larval abundance between oxygenated and deoxygenated bottom water has potentially great implications for depth preference and diel vertical movement as a strategy for upriver transport in estuarine systems prone to anoxia and hypoxia. In an estuary characterized by frequently anoxic deep waters, depth preference may not be an adaptively stable behavior. In such an estuary, one might expect to observe predominance of periodic vertical movements (STST or diel) over a shallower range of depths than in the Hudson. Depth preference would likely be less common due to the risks associated with anoxia.

Abundance of *G. bosci*

G. bosci is an abundant member of the Hudson River ichthyoplankton, but its abundance is highly variable between years. According to a yearly qualitative report of species presence or absence, no *G. bosci* specimens were collected in the Hudson River during annual Northeast Utilities sampling in 1975 and between 1977 and 1982 (Utilities report 2000). In the 1970s, freshwater flow was higher than normal and resulted in a higher abundance of freshwater species (utilities report, 1996). The successful freshwater species likely outcompeted *G. bosci* in its native habitat and led to its decline in the late 1970s. This trend reversed in the 1980s, when lower freshwater flow combined with higher dissolved oxygen levels at the mouth of the river (due to improved sewage treatment) allowed more marine species to enter the estuary. When anoxia occurs at the mouth of a river, it may act as an oxygen-depleted border preventing marine species from successfully entering the estuary. Perhaps adults were able to spawn there, but the more vulnerable larvae may have suffocated or suffered sub lethal effects as they tried to migrate upriver. *G. bosci* began its

recovery in 1983 and has been consistently represented in the ichthyofauna since then, though at unpredictable abundances.

The numerical rank abundance of G. bosci varies among East Coast estuaries, and it is difficult to compare population sizes due to temporally and mechanistically inconsistent sampling. *G. bosci* was the second most abundant species of fish in the ichthyoplankton samples that we collected. In the upper Chesapeake Bay and its tributaries, it was the most abundant species in the ichthyoplankton between 1963 and 1967 with an average abundance more than twice that of *Anchoa mitchilli* and accounted for 55.2% of all larvae collected (Dovel 1981). Abundance of *G. bosci* in the Hudson is somewhat less clear because most of the quantitative data on along-river distribution of the species is based on utility company sampling which did not differentiate between species of Gobiidae. However, the only other common Gobiid species in the Hudson is the seaboard goby, *G. ginsburgi*. Based on a complete lack of *G. ginsburgi* in our sampling effort and no observations of *G. ginsburgi* in utilities samples from 1998-99, it is likely that most of the larvae labeled as Gobiidae are actually *G. bosci*. Between 1988 and 1996, Gobiidae abundance in the Hudson River has fluctuated between 1,108 and 78,349 individuals collected over the season (**Fig. 12**) (Utilities report 2000). Juvenile gobies collected during these annual sampling efforts were identified to species. **Figure 13** illustrates how the annual catch of juvenile *G. bosci* has fluctuated between 1988 and1996. The number of juvenile *G. bosci* collected peaked in 1990 and dropped off drastically afterwards.

Apparent fluctuations in annual *G. bosci* population size may be due to actual change of the population or a result of inconsistent sampling protocol between years. The utilities

biweekly sampling was adjusted during each season to optimize collection of specific life stages of target species (yolk sac larvae and/or post-yolk sac larvae of Atlantic tomcod, bay anchovy, American shad, etc.) The regions and strata that were sampled were chosen to best represent whichever of these species needed to be collected during a particular sampling effort. In contrast, sampling in this experiment was specifically designed to collect bay anchovy (*Anchoa mitchilli*) . Therefore, our time-series survey should have produced a more temporally consistent sampling of the overall ichthyoplankton community structure. The utilities sampling was designed to collect data on economically important species, so techniques, times, and locations of sampling may have changed over the years to reflect this need. For this reason, it is difficult to conclude that changes in *G. bosci* population size are accurately reflected by available data. Based on the high rank abundance of G. bosci in our samples (second highest after *A. mitchilli*), it is clear that *G. bosci* is a dominant member of the ichthyoplankton during 1998 and 1999 in at least the portion of the Hudson that we sampled.

Based on longitudinal ichthyoplankton surveys in the Hudson between 1998 and 1996, *G. bosci* has become more abundant in 1998 and 1999 surveys (Utilities report 2000). Whether this is due to normal population fluctuation or reflects the beginning of a long-term trend towards higher larval density remains unclear. Because *G. bosci* was the second most abundant species collected in this ichthyoplankton survey, the presence or absence of larvae might be expected to have significant interactions with larvae of other species. For example, if *G. bosci* abundance is actually increasing, the estuary will be able to support less biomass of other larvae, particularly if space or food is a limiting factor.

Analysis of along-river movement

Due to the benthic spawning of *G. bosci*, it cannot be determined how far larvae move after hatching simply by comparing egg and larval distributions in ichthyoplankton samples. Unlike pelagic estuarine-dependent species in which the adults overwinter on the continental shelf (such as *A. mitchilli), G. bosci* is an exclusively estuarine species. Because eggs are attached to the substrate, they cannot be collected in ichthyoplankton samples and can only be retrieved with a benthic sled or by scuba diving. Spawning sites can be predicted by considering where the distributions of newly hatched larvae and oyster reefs necessary for spawning overlap. The absence of pelagic eggs means that age of a cohort of *G. bosci* larvae moving upriver cannot be determined by tracking distributions of eggs and larvae over time. It is therefore more difficult to determine how far any given individual may have migrated from its hatch site. Large individuals found upriver of small individuals may have arrived there by tidal transport, or they may have been spawned on that site and retained by behaving in one or more of the patterns mentioned above.

Based on regression analysis, growth rates (slopes of increment count versus length) varied most for smaller larvae. This indicates that conditions affecting growth of the youngest larvae may differ by year and date. It should be noted that this regression was of increment count vs. length rather than age vs. length because we do not know if increment counts are an accurate reflection of days since hatching in this species. For this reason, length at hatch cannot be determined by simply extrapolating the regression to its y-intercept. Length at hatch has been experimentally determined based on *G. bosci*

individuals from New Jersey (Able and Fahay 1998), but further investigation will be required before we can adopt these values for Hudson River estuary individuals

The otolith analysis will be further refined to provide an age-length regression model that can be used to track movement of cohorts (groups of individuals hatched on or near the same date) through time over the river. This will be done by determining if there are significant differences in growth rate between samples, and applying separate or pooled regressions of growth rate as appropriate. If the median position of a cohort moves upriver over time, then we will know that the behavioral mechanisms discovered in this experiment actually do contribute to upriver transport. Because growth rate of larvae varies by hatch season and productivity, application of a single age-length regression to all larvae may not accurately calculate the age of measured larvae. There were significant spatial and temporal variations in growth rate of bay anchovy *A. mitchilli*. Growth rates of larvae over 45 km and two years ranged between 0.39 to 0.88 mm d^{-1} (Jordan, Gospodarek et al. 1997). Because there is overlap in distributions of *G. bosci* and *A. mitchilli*, there is reason to expect that *G. bosci* growth rates may also vary temporally and spatially. By refining the regressions to year and bi-weekly specific patterns, we can determine the most appropriate and consistent way to determine individual and mean cohort age.

Differences in behavior and effect of spring mixing among two species

Vertical mixing of water during spring tide did not prevent larvae from having a strong depth preference or controlling their vertical position during periodic movements.

Turbulent mixing during spring tide is known to break down stratification of the water column (Peters 1997). If spring tide mixing decreased the ability of larvae to engage in periodic vertical movements or remain at depth, then rate of upriver transport of larvae should be slower during spring tide. This is not predicted based on our results. Although *G. bosci* larvae were generally deeper during neap tide than spring tide, homogenization of depth structure does not occur during spring tide. In order to determine the universality of *G. bosci's* transport behaviors, we compared them to those of the most abundant species in our samples, bay anchovy (*Anchoa mitchilli*). (Because *A. mitchilli* was far more abundant than *G. bosci*, analysis of A. mitchilli was based on all river sites rather than solely RS3). Both bay anchovy and naked goby are known to migrate upriver, but the mechanisms that they use are different (Schultz, Lwiza et al. in review). *G. bosci* appears to use depth preference and diel vertical movements (dependent upon hydrography in the Hudson, as explained above), whereas *A. mitchilli* uses depth preference. Depth distribution of *A. mitchilli* became homogenized during spring tide. This indicates that *G. bosci* should have a higher overall rate of upriver transport than *A. mitchilli* because *G. bosci* transport rate is less dependent upon stratification of the water column. This difference in transport rates and mechanisms illustrates that two species that occur together in the ichthyoplankton do not necessarily have such concurrent distributions as a result of engaging in the same behaviors. When analyzing patterns of larval distribution, it is important to consider the behavioral mechanisms of each species individually rather than assume that the factors that affect the distribution of one species will necessarily be identical in others.

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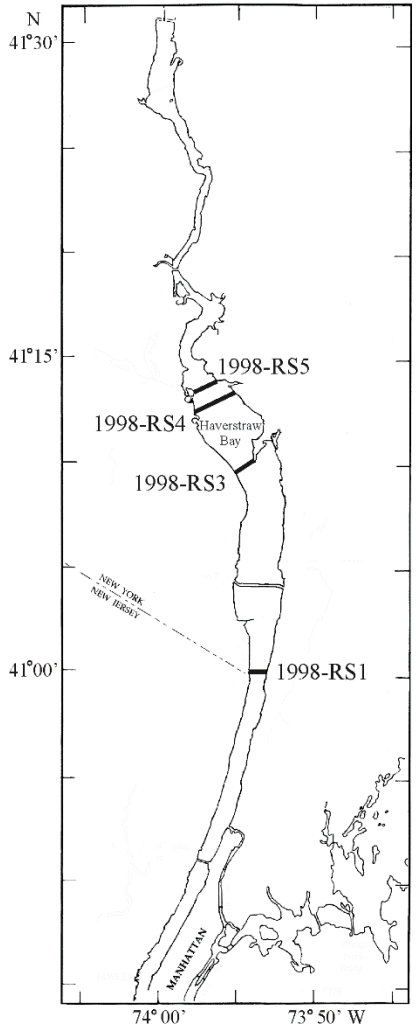

Figure. 1: Sampling area in the Hudson River estuary, eastern New York State. Solid bars represent transect sites. Specimens discussed in this thesis were collected at RS3.

Figure 2: A Tucker trawl was used to sample four discrete depths: 2, 4, 6, and 8 m.

Table 1: Tidal stage and duration of cruises

Cruise	M_f tide stage	1998-RS3
1998-C1	Spring	7/23 1500 - 7/26 0600
1998-C2	Neap	7/28 1800 - 7/31 1800

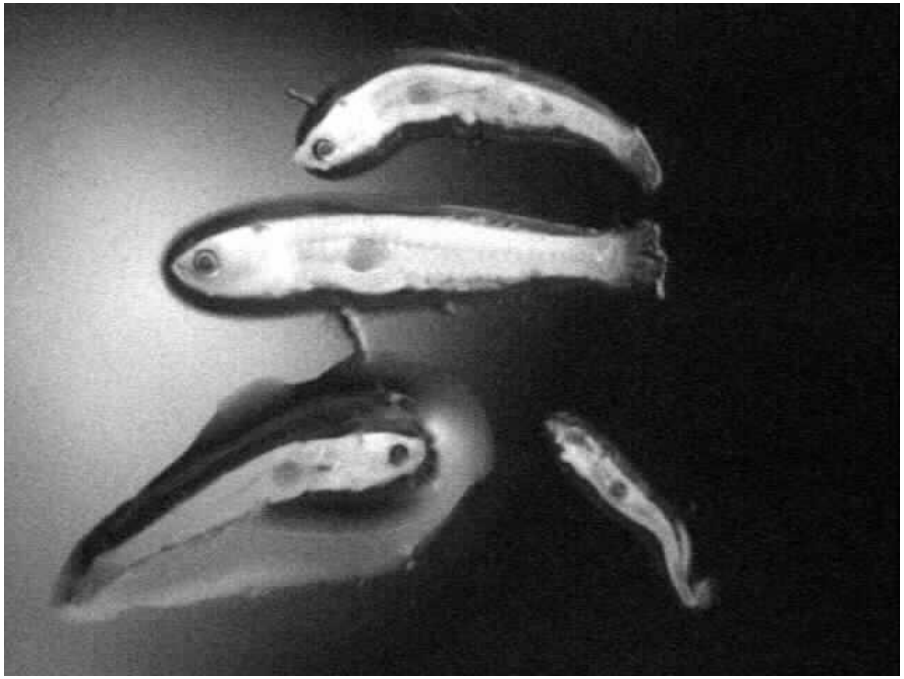

Figure 3: Larval *G. bosci* viewed with Optimas image analysis system. Video images of larvae were frozen and exported to a computer for calibrated on-screen measurement.

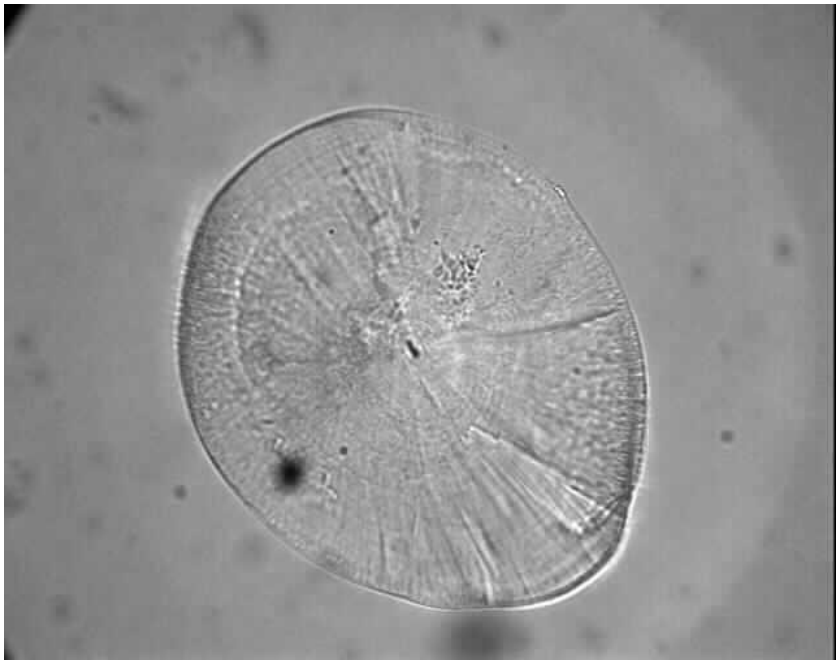

Figure 4: A *G. bosci* sagittal otolith viewed at 400x magnification. Dark rings are daily growth increments.

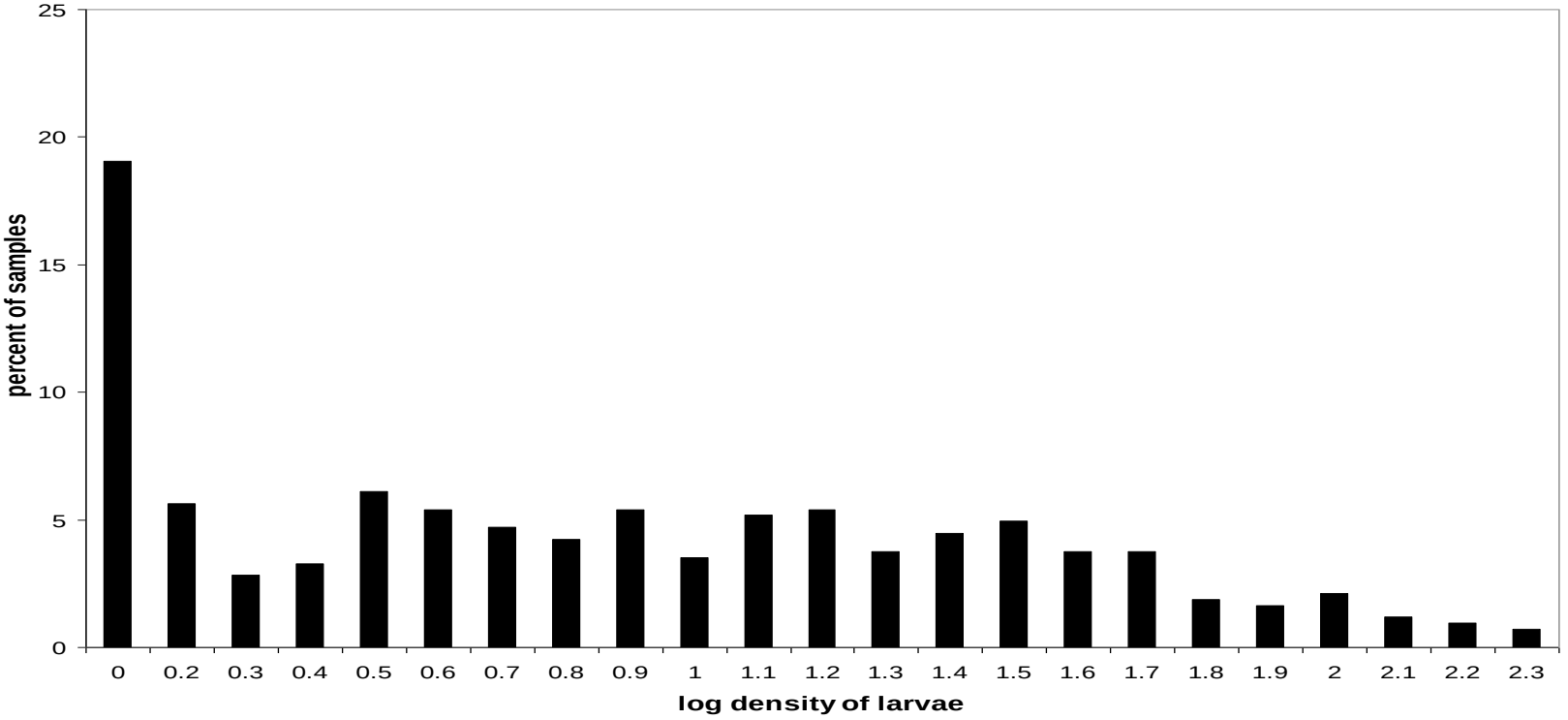

Figure 5: Sample density distribution of larvae. The majority of samples had no *G. bosci* larvae.

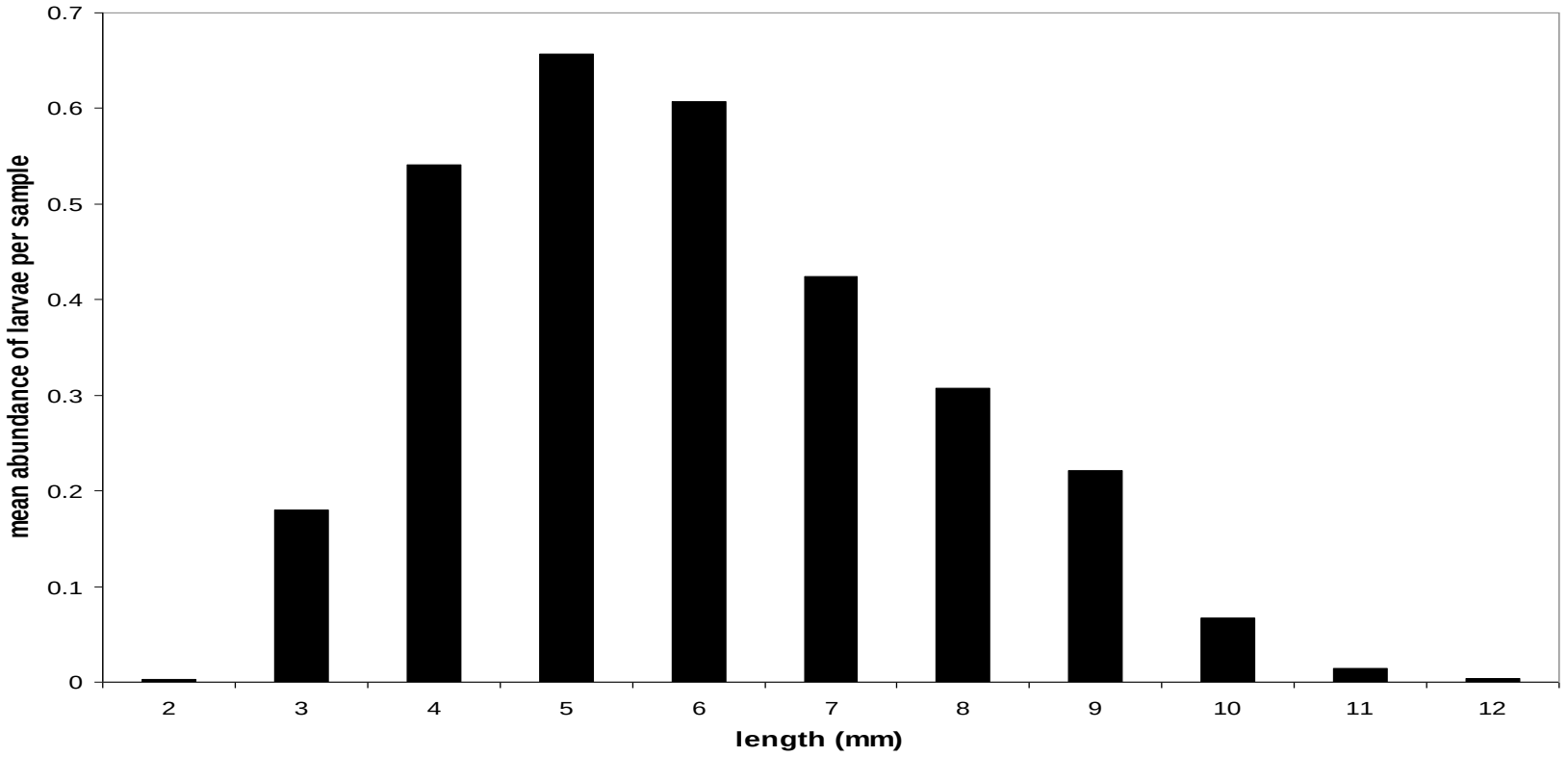

Figure 6: Mean sample length distribution of larvae. Larvae were divided into 2 size classes: small (less than 5 mm) and large (greater than or equal to 5 mm)

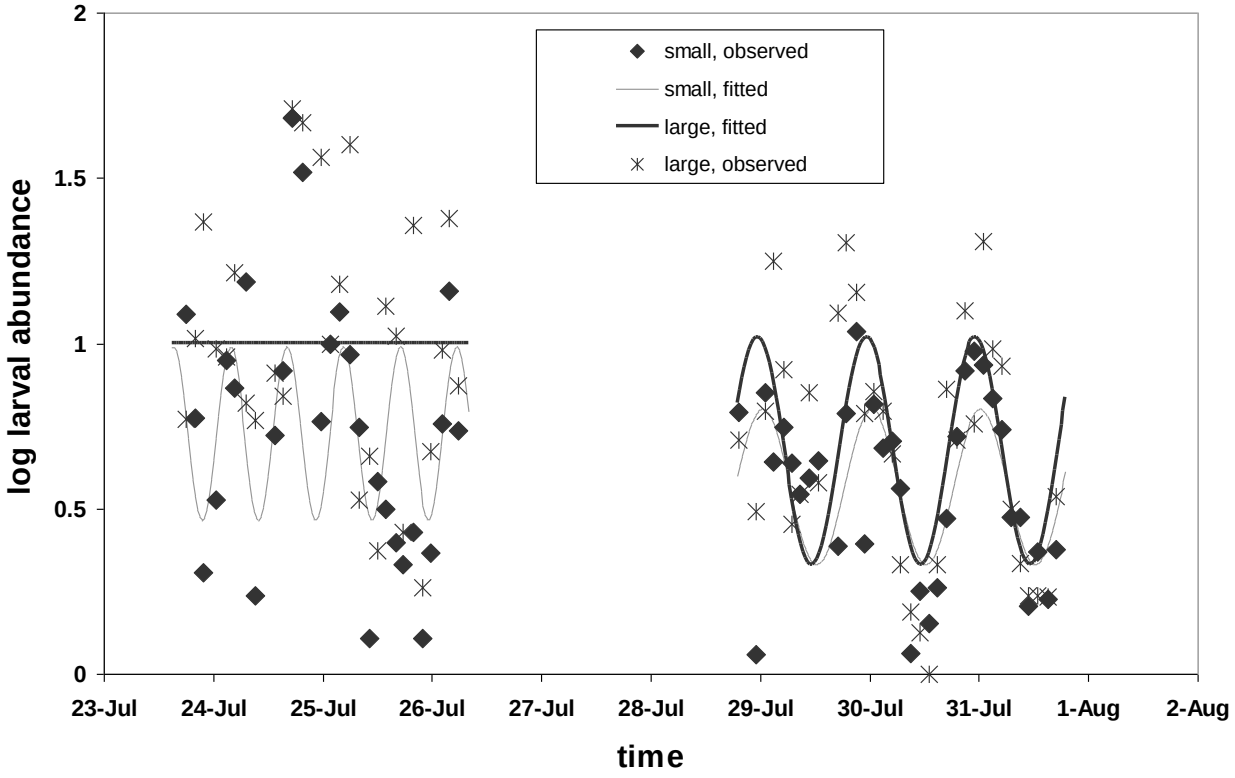

Figure 7: Temporal variability in mean log abundance of larvae per sample, by size and cruise. July 23 - 27 is spring tide; July 29 - Aug. 1 is neap tide. Lines represent regressed values; points are mean larval abundance per sample at time x.

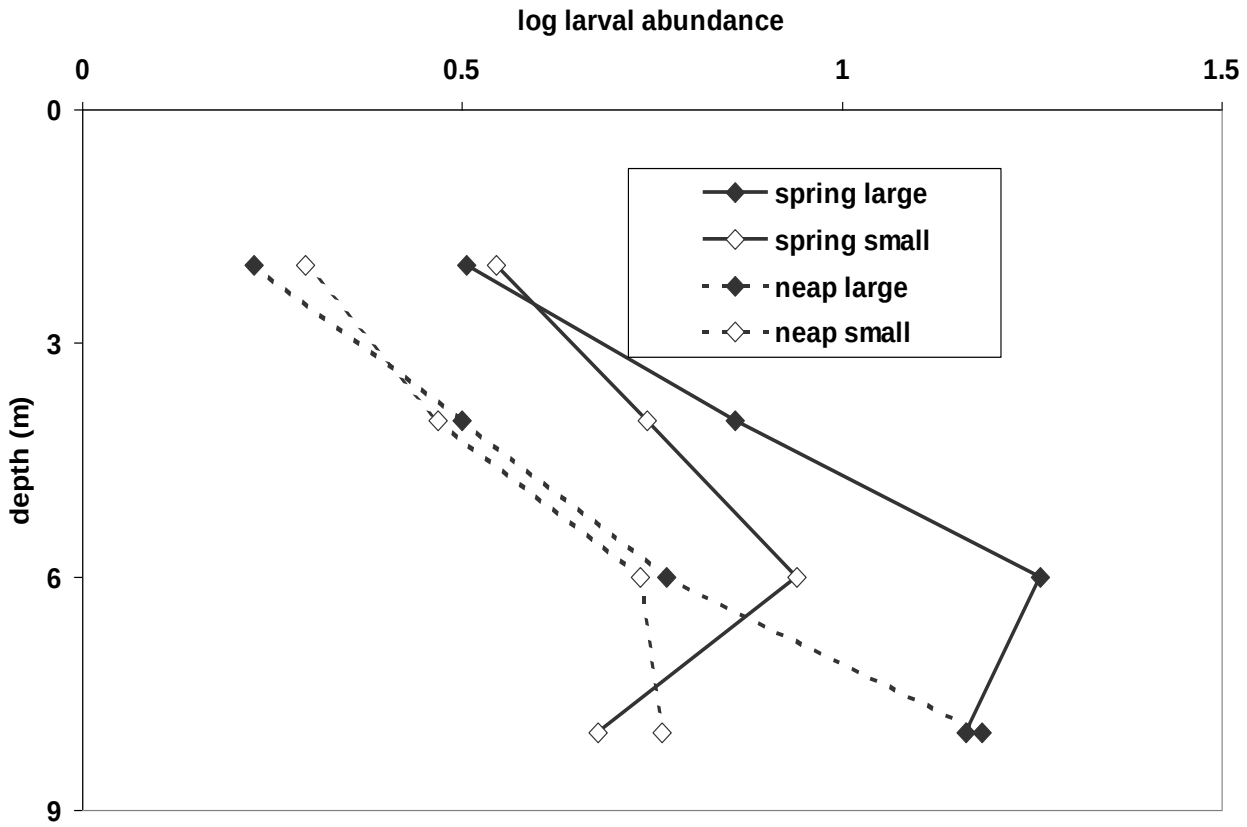

Figure 9: Variability in larval abundance with depth. Each point represents mean abundance of large or small larvae in samples at that depth.

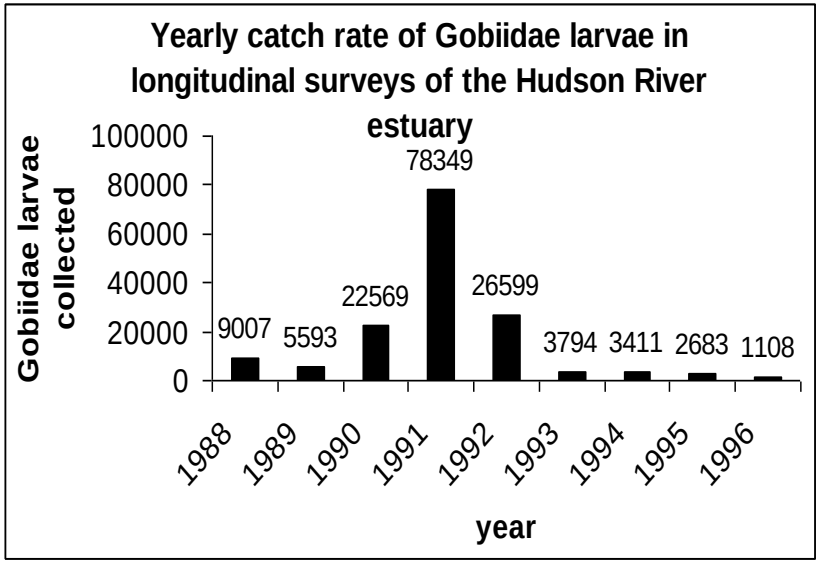

Figure 10: Annual abundance of Gobiidae larvae collected during utilities company longitudinal ichthyoplankton sampling. Larvae were not identified to genus or species level. Larval counts are not adjusted for water volume sampled.

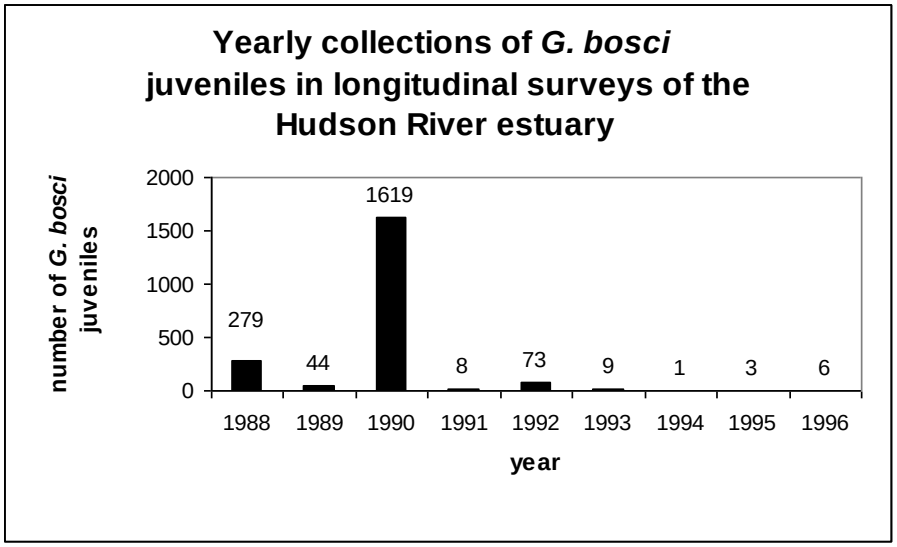

Figure 11: Annual abundance of *G. bosci* juveniles collected during utilities longitudinal ichthyoplankton sampling. Juvenile counts are not adjusted for water volume sampled.

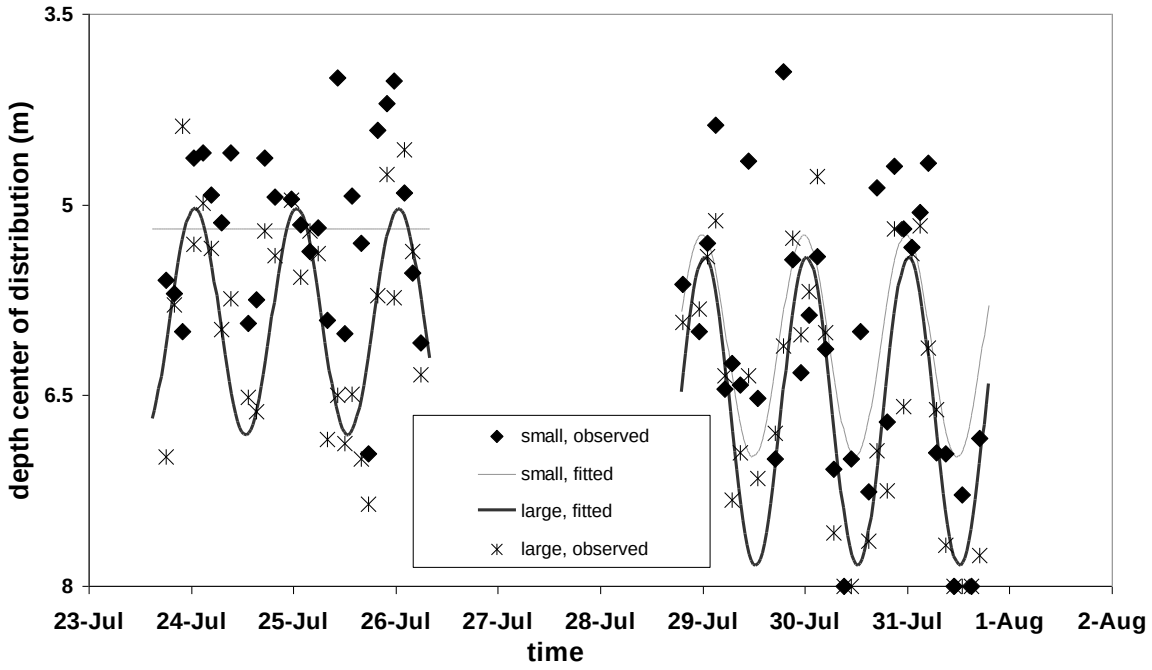

Figure 11: Temporal variability in depth center of larval distribution, by size and cruise. July 23 - 27 is spring tide; July 29 - Aug. 1 is neap tide. Lines represent regressed values; points are mean depth distribution of actual samples at time x.

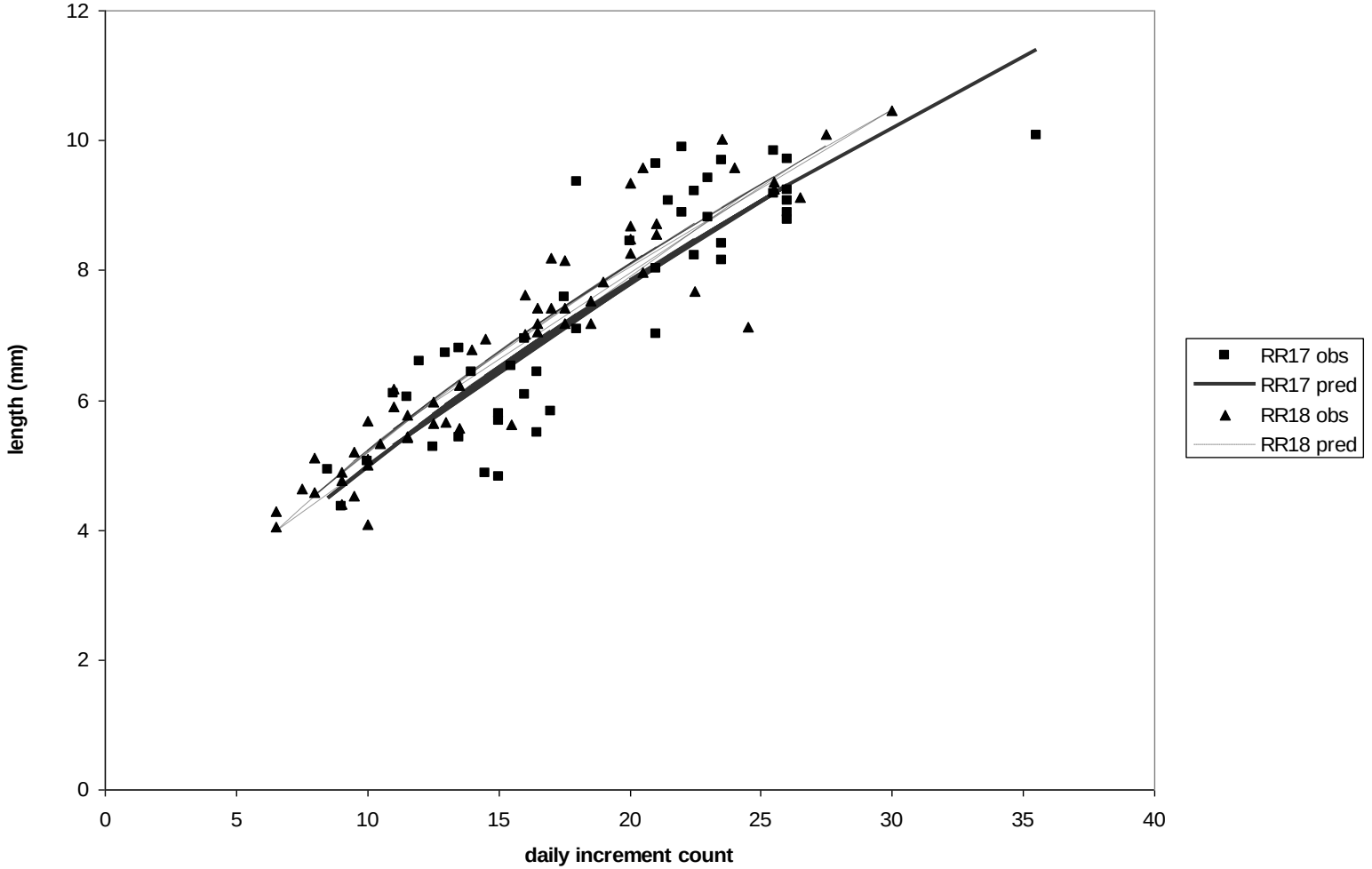

Figure 12: Observed and predicted count-length regression for RR17 & RR18 in 1998. RR17 = July 14; RR18 = July 28. Predicted values are expected values based on regression of increment counts and corresponding standard lengths of larvae collected on these dates.

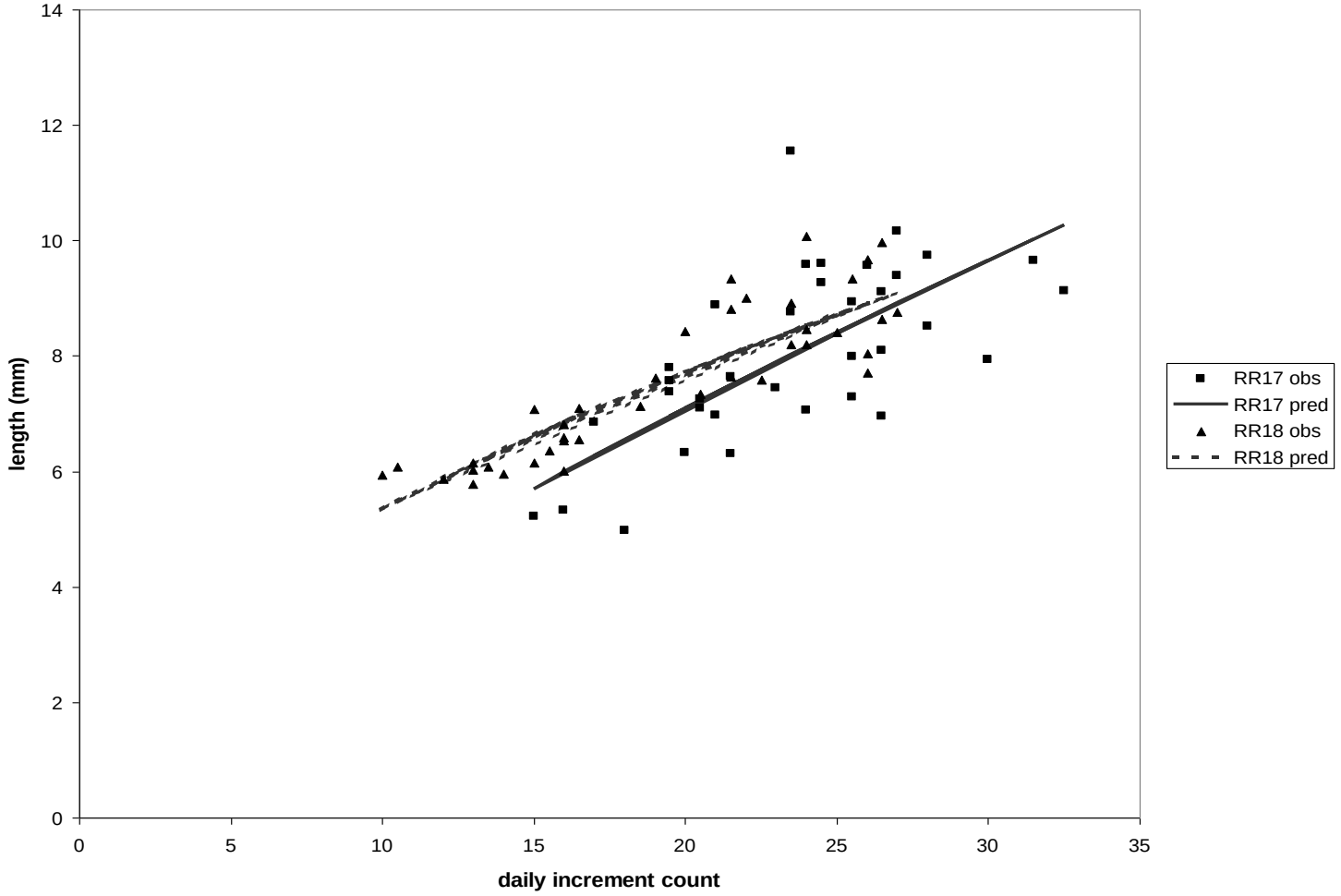

Figure 13: Observed and predicted count-length regression for RR17 & RR18 in 1999. RR17 = July 12 - 13; RR18 = July 26 - 28. Predicted values are expected value based on regression of increment counts and corresponding standard lengths of larvae collected on these date.

Table 2: ANOVA of significant predictors for variability in abundance between depths by cruise

Source	SS	MSE	F Value	Pr > F
Cruise 1:				
depth	1.7	0.87	3	0.055
xm2	1.2	1.2	4	0.047
Cruise 2:				
depth	1.1	1.1	6.4	0.013
dayt2	0.5	0.5	3.1	0.085
xk1	2	2	12	0.0008
zm2	3.8	3.8	23	<.0001

Cruise 1 ANOVA is based on 99 samples from 4, 6, and 8 m. Cruise 2 ANOVA is based on 77 samples from 6 and 8 m. Other depths (2 m in C1, 2 and 4 m in C2) were excluded from analysis due to an excessive number of samples from these depths that contained zero larvae. The F value is used to decide whether the sample means are within sampling variability of each other. P values indicate the significance of a predictor in the model. All numerical values presented all tables henceforth are rounded to 2 significant figures.

Table 3: ANOVAs for variability in sample abundance of larvae

	variable	parameter est.	std error	SS	F value	Pr > F
spring large	no significant predictors					
spring small	Intercept	0.73	0.067	15	120	<.0001
	xm2	-0.26	0.095	0.96	7.7	0.01
neap large	Intercept	0.68	0.049	16	190	<.0001
	xk1	-0.3	0.07	1.5	18	0.0002
neap small	Intercept	0.56	0.042	11	180	<.0001
	zk1	-0.17	0.059	0.49	8.3	0.0072

Significant p values indicate that these tidal components are significant predictors of variability in sample abundance of larvae. Model R-square values express the cumulative amount of variability explained by the predictors. (*Add R-square values to this table; delete next table. Do same for Zcm ANOVA*)

Table 4: Summary of stepwise regression for temporal variability in sample abundance of larvae.

		Partial	Model		
	Variable	R-Square	R-Square	F Value	Pr > F
spring large	no significant predictors				
spring small	xm2	0.23	0.23	7.7	0.01
neap large	xk1	0.36	0.36	18	0.0002
	zk1	0.12	0.48	7.3	0.011
neap small	zk1	0.21	0.21	8.3	0.0072
	xk1	0.19	0.39	9.7	0.004

Partial R-square is the amount of temporal variability in abundance of larvae that is explained by each predictor. Model R-square is the cumulative amount of variability explained by both predictors (if more than one predictor) in each model.

Table 5: ANOVAs for variability in larval depth center of distribution

	variable	parameter est.	std error	SS	F value	Pr > F
spring large	Intercept	5.9	0.13	950	2100	<.0001
	zk1	0.63	0.17	5.9	13	0.0013
spring small	no significant predictors					
neap large	Intercept	6.6	0.14	1400	2100	<.0001
	zk1	0.87	0.21	12	18	0.0002
neap small	Intercept	6.09	0.17	1300	1300	<.0001
	xk1	0.7	0.24	8.4	8.9	0.0055

	Variable Entered	Partial R-Square	Model R-Square	F Value	Pr > F
spring large	zk1	0.33	0.33	13	0.0013
	xk1	0.25	0.58	15	0.0007
spring small	no significant predictors				
neap large	zk1	0.37	0.37	18	0.0002
	xk1	0.33	0.7	33	<.0001
neap small	xk1	0.22	0.22	8.9	0.0055
	zk1	0.12	0.33	5.5	0.026

Table 6: Summary of stepwise regression for temporal variability in center of larval depth distribution. Xk1 and zk1 are the two components of the k1 (23.9 hr period) tide, as explained in methods. Partial R-square is the amount of temporal variability in depth center of distribution that is explained by each predictor. Model R-square is the cumulative amount of variability explained by both predictors in each model.

	Source	SS	MSE	F value	Pr > F
RR 17 1998	logcount	0.31	0.31	190	<.0001
	sample	0.019	0.0097	5.9	0.0056
	logcount*sample	0.015	0.0076	4.6	0.015
RR 18 1998	logcount	0.5	0.5	430	<.0001
	sample	0.0059	0.003	2.6	0.087
	logcount*sample	0.0072	0.0036	3.1	0.053
RR 17 1999	logcount	0.1	0.1	37	<.0001
	sample	0.0047	0.0047	1.7	0.2
	logcount*sample	0.0057	0.0057	2.1	0.16
RR 17 1999	logcount	0.17	0.17	194	<.0001
	sample	0.00037	0.00037	0.43	0.51
	logcount*sample	0.00087	0.00087	1	0.32

Table 7: ANCOVAs by year and date (RR = river run) to determine significant regressors for growth rate slope for along-river analysis. P value less than 0.05 for "sample" indicates significant variability among samples within a year/RR class. SS = sum of squares, MSE = mean square error.

	R^2	mn length	Variable	Param. est	Std err	t value
RR 17 1998	0.76	0.86	Intercept	0.044	0.071	0.62
			logcount	0.65	0.056	12
RR 18 1998	0.9	0.82	Intercept	0.039	0.025	1.6
			logcount	0.67	0.02	33
RR 17 1999	0.58	0.9	Intercept	-0.12	0.1	-1.2
			logcount	0.74	0.076	9.7
RR 18 1999	0.8	0.87	Intercept	0.19	0.04	4.7
			logcount	0.54	0.031	17

Table 8: Regression statistics for RR 17 1998 (N = 46 individuals), RR18 1998 (N = 58), RR17 1999 (N = 35), and RR18 1999 (N =39).